Water uptake by trees in a riparian hardwood forest (Rhine floodplain, France)

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Abstract:

Water flow in the soil–root–stem system was studied in a flooded riparian hardwood forest in the upper Rhine floodplain. The study was undertaken to identify the vertical distribution of water uptake by trees in a system where the groundwater is at a depth of less than 1 m. The three dominant ligneous species (*Quercus robur, Fraxinus excelsior* and *Populus alba*) were investigated for root structure (vertical extension of root systems), leaf and soil water potential (Ψ_m), isotopic signal (^{18}O) of soil water and xylem sap. The root density of oak and poplar was maximal at a depth of 20 to 60 cm, whereas the roots of the ash explored the surface horizon between 0 and 30 cm, which suggests a complementary tree root distribution in the hardwood forest. The flow density of oak and poplar was much lower than that of the ash. However, in the three cases the depth of soil explored by the roots reached 1·2 m, i.e. just above a bed of gravel. The oak roots had a large lateral distribution up to a distance of 15 m from the trunk. The water potential of the soil measured at 1 m from the trunk showed a zone of strong water potential between 20 and 60 cm deep. The vertical profile of soil water content varied from 0·40 to 0·50 cm^3 cm^{-3} close to the water table, and 0·20 to 0·30 cm^3 cm^{-3} in the rooting zone. The isotopic signal of stem water was constant over the whole 24-h cycle, which suggested that the uptake of water by trees occurred at a relatively constant depth. By comparing the isotopic composition of water between soil and plant, it was concluded that the water uptake occurred at a depth of 20 to 60 cm, which was in good agreement with the root and soil water potential distributions. The riparian forest therefore did not take water directly from the water table but from the unsaturated zone through the effect of capillarity.

KEY WORDS groundwater; riparian forest; stable isotopes; root density; soil water; sap flow

INTRODUCTION

Riparian forests are often dominated by woody phreatophytes, which require the presence of groundwater. Floodwater saturates the soil and creates anaerobic conditions but may damage the roots. Little is known about the vertical distribution of roots and water uptake in flooded areas where the groundwater level is close to the soil surface. More or less flood-tolerant woody species have adapted to grow in this environment (Blom, 1999). They develop several adaptative traits: morphological (i.e. surface rooting, root extension), physiological (i.e. stomatal closure, nutrient uptake, etc.) or biochemical (i.e. regulation of gas exchanges) (Armstrong *et al*., 1994).

Root distribution of trees is usually seen as the main indicator of competition between trees assuming that for an equal supply of growth resources in the soil, resource uptake is related to the amount of root biomass (Belmans *et al*., 1979). Similarly, most forest water-uptake models assume that water extraction rate is closely related to root density (Rowse *et al*., 1978; Belmans *et al*., 1979). This relationship between water extraction and root density is also used in agroforestry models (Mayus *et al*., 1999; Mobbs *et al*., 1998).

In riparian forests, the soil water content is close to saturation because of the proximity of the groundwater, and the roots are well provided with water. Therefore, available water can be assessed by comparing the isotopic composition of sap with that of potential water sources in the soil. The isotopic composition of sap is commonly used as a measurement of the isotopic signature of the water uptake by plants in the soil (e.g. Wershaw *et al*., 1970; White *et al*., 1985; Dawson & Ehleringer, 1991; Walker & Richardson, 1991). No isotopic fractionation of oxygen and hydrogen occurs during soil water uptake by roots (Washburn & Smith, 1934; Zimmerman *et al*., 1967; Thornburn *et al*., 1992; Bariac *et al*., 1994). Gradients in the isotopic composition of water within soil profiles arise because of differences in the seasonal input of rainwater into the soil and evaporation in the surface layers.

The objectives of this study were two-fold. Firstly an understanding of the partitioning of groundwater resources by plants species in the flooded forests was needed, by identifying the zones of root uptake and

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monitoring the spatial variations in the soil profile. The relationships between the water status in the different soil layers and the pattern of the root distribution are prerequisites for determining the distribution of available water which can be theoretically absorbed by plants. But, root presence may not be a reliable indicator of water uptake in the soil layers as has been shown by Plamboeck *et al*. (1999). In this context, a second objective was to compare different methods for analysing water uptake. Thus the use of root distribution analysis, ^{18}O gradients in soil water and tree sap, water potential of plant and soil, and xylem sap flow were combined. Sap flow, leaf and soil water potential measurements enabled the determination of the availability of water and the efficiency of trees at absorbing water depending on the depth in the soil profile.

MATERIAL AND METHODS

Site descriptions

Experiments were conducted in the Rhine alluvial valley (eastern France) (latitude 58°37′ and longitude 5°57', mean elevation 160 m). The climate of the region is classified as sub-continental characterized by low relative air humidity in spring and summer. Mean annual temperature is 9·7 °C and average annual rainfall of about 576 mm (mean for the period 1951–1980). The water table is on average 1·3 m below the soil surface except during flooding.

The study site was an artificial island, named Rhinau Island (length: 15 km, width: 0·5 km), bordered by the main Rhine channel (straightened in 1860) and the Large Canal built in 1963. The hydrological regime of the Rhine in this part of the upper course is characterized by high water between May and August and low water between November and March, with a mean annual flow of 1050 $m^3\ s^{-1}$ (calculated between 1934 and 1990). The island is flooded by slow-flowing waters, whenever the river flow exceeds 2500 $m^3\ s^{-1}$.

The natural, strong morphogenesis of the Rhine ended with the river being straightened in 1860. Since then, silt and clay carried by the river has covered the island with about a metre of fine texture deposits, overlying the gravel and sand. The soil is an alluvial loam. The soil water content at saturation was approximately 0·415 $cm^3\ cm^{-3}$ on average in the upper 100 cm of soil. The bulk density was about 1·4 g cm^{-3}. The soil is calcareous (25% total carbonate, pH >7·5) and young (fluent A/C type, USDA), it is silt to silt-clay in the upper horizon (10% sand, 60% silt and 30% clay) with increasing sand content with depth (85% sand, 10% silt and 5% clay); it becomes coarse-textured with greater depth (>1 m: sand and gravel).

The site is home to several communities consisting of pure stands of short-living softwood trees (*Salix alba, Populus nigra, Populus alba*) and a mixed canopy of long-living, eutrophic and co-dominant hardwoods (mainly *Quercus robur, Fraxinus excelsior, Ulmus minor*; Margl, 1973; Carbiener and Schnitzler, 1990; Oldeman, 1990). On the Rhinau Island, the dominant species were ash (*Fraxinus excelsior* L.), oak (*Quercus robur* L.) and white poplar (*Populus alba* L.). The characteristics of the riparian forest are shown in Table I.

Experimental design

Within each dominant species, trees were sampled according to the basal area (Table II). The sample for sap flow was limited to two oaks (Q38 and Q90; 87% of total basal area occupied by oaks), one white poplar (P77, 67% of total poplar basal area) and three ash trees (F472, F502 and F53; 70% of the total ash basal area). Two supplementary individuals (Q23 and Q26) were sampled for the root architecture to have a representative sampling of the study site, despite the variability of the depth of the gravel (between 0·8 and 1·4 m). Q90, Q26 and P77 were used for measurements of the isotopic composition of water in the collar, and only Q26 for the isotopic composition of the lateral roots. All measurements were made at low water table, its height remaining constant at about 1·3 m from the mean surface of the soil.

Root architecture

The vertical distribution of the root system was described *in situ* during two days in July 1995 and 1996 in the Rhinau Island. A portion of the soil (1·2 m wide) was excavated at 1 m from the trunk down to the gravel level. The total soil area prospected for roots was a length of 1·2 m down to the depth of the gravel. Gravel depth varied from 0·8 to 1·4 m deep depending on the surface relief. The area of the section prospected therefore represented 0·96 to 1·98 m^2. Among the individual trees selected, three oaks (Q90, Q23 and Q26), two

Table I. Biometric characteristics of the riparian forest trees of Rhinau Island

	Basal area ($m^2\ ha^{-1}$)	Density (trees ha^{-1})	Canopy area ($m^2\ ha^{-1}$)	Mean tree age (years)	Mean height (m)	Mean diameter[a] (cm)
Quercus robur	11·07	20	2914	130	22	83
Populus alba	5·08	16	1688	80	26	60
Populus nigra	0·34	1	—	—	—	62
Fraxinus excelsior	13·07	344	6324	60	21	18
Populus tremula	0·5	5	—	—	—	35

[a] Mean diameter was measured 1.3 m above ground.

Table II. Number of trees per diameter class[a]

Trunk diameter classes (cm)	Number of trees per diameter class			Percentage basal area per class		
	Oak	Poplar	Ash	Oak	Poplar	Ash
5–20			22			16·0
20–30			3			8·7
30–40			1			6·1
40–50		3	3		9·0	*31·1*[b]
50–60		2	1		9·3	*15·7*
60–70	3		1	13·8		*22·4*[b]
70–80	5	8		*29·8*[b]	*67·1*[b]	
80–90						
90–100	6	1		*56·6*[b]	14·6	
Total	14	14	31	*100*	*100*	*100*

[a] The total surface area of the island was about 8 km^2; here a plot of 5600 m^2 was investigated. The whole plot was considered for oak and poplar, but owing to the higher density of small ash, only a subplot of 800 m^2 was sampled. Italic typeface indicates diameter class of trees studied for sap flow measurements.
[b] The diameter class of trees studied for root structure.

ashes (F502 and F53) and one poplar (P77) were studied (Figure 1). For oak Q90 and poplar P77, two supplementary pits were excavated 2 and 3 m from the trunk and the lateral distribution of the roots was analysed for a root 15 m from the trunk, because of the lateral extension of these two species.

After excavation with a mechanical digger, the soil sections were evened, and brushed to clear the roots along 10 or 20 mm length, and make them more visible. Roots were counted every 100 mm using a steel grid, from the soil surface to the bottom of the vertical face of the trench. They were classified into: diameter 1–5 mm (fine roots), 5–20 mm (medium roots), 20–50 mm (coarse roots) and >50 mm (very coarse roots) according to Böhm (1979). Root diameter was measured using a calliper.

The root area was computed for each soil layer and each diameter class. An average area for roots <50 mm was assigned. The surface area of very coarse roots (>50 mm) was assessed directly in the field using the calliper. Roots observed in the trench wall generally remained in the same soil horizon over a distance of 10 cm. Assigning an average density to each root volume assessed root biomass. Individual root density was calculated for five replicates per root class. It was assessed by estimating the root volume and root mass after drying (7 days at 70 °C in an oven). Root density (oven-dry) was 0·70 g cm^{-3}. The differences of density between the classes of root were not significant. To calculate the biomasses in 1 dm^3 of earth, roots observed on the section were considered to be regular cylinders 10 cm long. The mass of a root 10 cm long was 0·7 g for fine roots, 8·6 g for medium roots, 67·3 g for coarse roots and 137·4 g for very coarse roots.

Although it was not possible to distinguish live roots from dead ones in the field with sufficient reliability, it

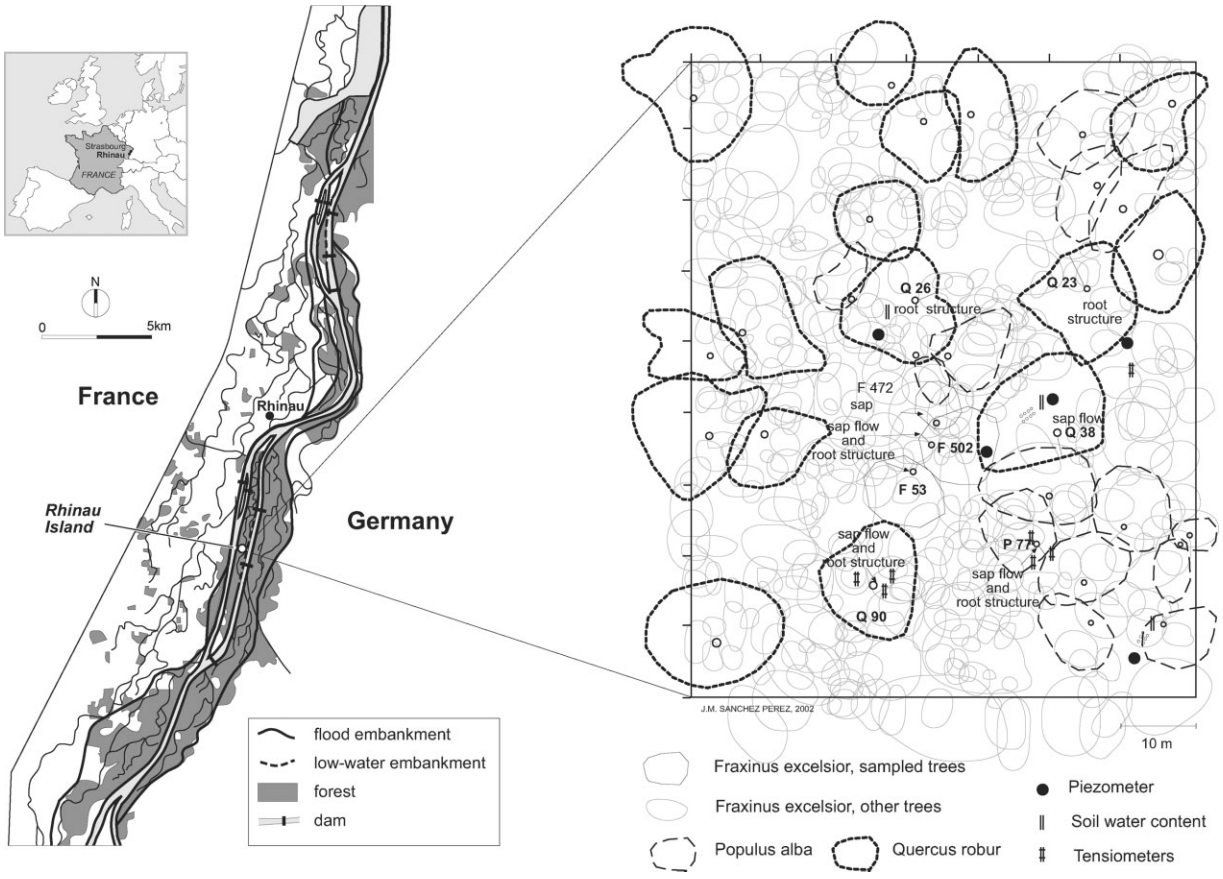

Figure 1. Location of the study area, crown map of field plot (for clarity, the non-sampled ash trees are shown in very light grey) and field equipment

was easy to identify roots of herbaceous plants, oak, ash and poplar by morphological and physical characteristics (colour and flexibility). It was checked that there was no vertical taproot by excavating the soil up to the trunk after measurements were complete in the trench.

Isotopic composition of xylem and soil water

The origin of the water taken up by the trees was identified by sampling sapwood in the tree on an hourly basis and comparing the isotopic signatures of the sap and the soil water. The sapwood samples were taken between 8 : 00 a.m. and 18 : 00 p.m. The sap was collected 0·5 m from ground level by coring in the trunk of the tree and by removing the outer bark (core diameter 6 cm). The volume of sap for each sample was between 0·5 and 0·8 ml. In the pit used for the root architecture analysis, soil samples were collected with an auger every 5 cm down to 20 cm and then every 10 cm down to 1·40 m depth. In the same pit, root samples were collected at every 10 cm depth. Roots, sapwood and soil samples were immediately placed in glass vials with tight sealing caps and stored at $-8\,^{\circ}$C.

Water was extracted from the soil, root and sapwood samples during 14 h cryogenic vacuum distillations, and sealed in closed glass containers. Oxygen-isotope composition was measured by isotope ratio mass spectrometry after CO_2–H_2O equilibration using the Epstein and Mayeda (1953) technique. Results were expressed relative to a standard (V-SMOW; Gonfiantini 1978) using delta notation (δ) where $\delta^{18}O$ is given by:

$$\delta^{18}O = \frac{R^{18}O_{sample} - R^{18}O_{V-SMOW}}{R^{18}O_{V-SMOW}}$$

where the values of $R^{18}O_{sample}$ and $R^{18}O_{V-SMOW}$ are the $^{18}O/^{16}O$ for the sample and V-SMOW, respectively. As the difference between samples and standard is small, the 'δ -value' is usually expressed in parts per thousand.

Sap flow measurements

Sap flow measurements were made by Granier's method: two flux sensors (30–40 mm long, 2 mm diameter) with a 20-mm zone of heating wire were inserted radially into the trunk with a vertical spacing of 15–20 cm (Granier, 1985, 1987). A sensor couple was located in the trunk at a height of 1·2 m from the soil and in the roots at 1·2 m from the trunk, the upper one was heated constantly at 0·2 W, and the lower one was unheated. The temperature difference (ΔT) between the two probes was related to sap flux density (sap flow per unit of sapwood area F, was expressed as dm^3 H_2O dm^{-2} sapwood area h^{-1}) in the vicinity of the heated probe. Temperature differences were related to the mass flow of water via an empirical calibration performed with a trunk section from several tree species (Granier, 1985). This relation can be described by:

$$F = 4{\cdot}28 * \left(\frac{\Delta T_M}{\Delta T} - 1\right)^{1{\cdot}23}$$

where ΔT_M is the difference in temperature measured between the two sensors at zero flow (night values) and ΔT is the difference in temperature at positive flow conditions ($F > 0$) at a given time. Total sap flow S is calculated as the product of F and the sapwood area of the tree (total sap flow was expressed in $l\,h^{-1}$ or $l\,day^{-1}$). The sapwood area was measured at breast height directly from radial cores. The sapwood–heartwood transition was located by viewing the cores against diffuse light, sapwood being translucent and heartwood opaque.

The signal of the sap flux sensor was measured every 10 s and the average was recorded every 30 min by a datalogger (Campbell CR10, Campbell Scientific Inc., USA) during the growing period (May to October in 1995 and 1996).

Sap flux density was simultaneously measured in the trunk and in three roots from two individual trees (one oak, Q 90 and one poplar, P 77) from 26 June to 21 November 1996, in order to evaluate the contribution of large-diameter roots to stem sap flow: the mean F of the three root classes was multiplied by the total calculated area of root sapwood and compared to the stem sap flow (S).

Water potential (soil and plant) measurements

Leaf water potential was measured using a pressure chamber (Soil Moisture Co., Santa Barbara, CA, USA) on three stems from the crown of each tree every 2 h. The measurements were made on 10 sun-exposed leaves of six oaks and three ashes in July 1995 and of five oaks in 1996.

Water content in the soil, was expressed on the basis of soil and water mass or soil and water volume. Mass water content is the ratio of water mass to dry soil mass. Volumetric water content is the volume of water per volume of soil. Volumetric soil water contents were measured by time-domain reflectometry (TRIME System, IMKO, Germany) in the pits excavated for the root structure measurements with a three-rod probe (length = 80 mm, rod diameter = 3·5 mm, separation between rods = 20 mm) every 5 cm down to the level of the gravel.

The soil water potential was monitored with four groups of tensiometers per tree located 1 m from the trunk (measurements were made on oak Q90 and poplar P77), at the following depths in the soil profile: 15, 25, 35, 55, 75 and 95 cm. Measurement of soil water pressure was made with tensiometers using an electronic pressure transducer (model SKT 650, SDEC France, Tours, France) equipped with a syringe needle to pierce the tensiometer septum. Measurements were made from 26 June to 21 November 1996.

RESULTS

Root structure

The mean root density for the soil profile studied represented 524 g cm^{-3} for oak, 439 g cm^{-3} for poplar and 94 g cm^{-3} for ash. The roots of oaks occupied the

ground down to 1·4 m deep, or at least down to the pebbles. Root density reached its maximum between 30 and 40 cm deep 1 m from the trunk; this includes the highest density of roots of large diameter (>50 mm), these very coarse roots extended from 10 to 70 cm deep (Figure 2). In the first 10 cm of soil, there was less than 0·1% root (roots of diameter <20 mm). Only roots <50 mm occurred below 70 cm depth and only <20 mm roots below 90 cm. The vertical distribution of the oak roots varied according to the distance from the trunk. The root densities decreased by a factor of more than six as the distance from the trunk increased from 1 to 3 m. The colonized depth was 80–90 cm at a distance of 3 m. The maximum root density occurred between 50 and 60 cm deep 3 m from the trunk and 40–50 cm deep 2 m from the trunk. Roots showed necrosis at depths of 90 cm to 1·1 m, i.e. in the strongly anaerobic horizon, before the level of the pebbles. The extraction of a large root and one of its ramifications over a horizontal distance of 14 m shows that the spreading depth remained almost constant for main roots at a depth of 45 to 55 cm (Figure 3).

The root system of the ash trees presented a similar structure, in spite of differences in the vertical distribution of the densities (Figures 2). The root system grew down to the pebbles (90–100 cm). Its vertical distribution presented two density peaks, the first at a depth of 0 to 20 cm and the second 40 to 60 cm. The roots that occupied the soil in depth were oblique roots and their ramifications were vertical and horizontal. Roots of diameter 20–50 mm did not occur in the strongly anaerobic horizon, which was only colonized by roots of diameter less than 20 mm. The excavations dug 1 m from the trunk showed that only the large roots close to the surface (0–20 cm) extended over more than 2 m from the trunk. The maximum extension of these roots was around 5 m.

The roots of the poplar, at 1 m from the trunk, reached 110 cm depth, i.e. down to the pebbles (Figure 2). The highest density of roots occurred at a depth of 30 to 60 cm, i.e. the depth where very coarse roots (>50 mm) were most abundant. The first 10 cm of soil was sparsely occupied with less than 0·1% of the roots (fine roots of diameter <5 mm). In the layer 10–20 cm deep few roots (<5 mm) occurred. At depths of 30 to 60 cm, the root diameter was >50 mm. Roots of diameter 20–50 mm, which correspond to the main ramifications of vertical roots, were only present from 70 to 80 cm. At a distance from the trunk of between 1 and 3 m, the distribution of roots shifted towards the surface of the soil. Very few roots occurred at a depth of more than 60 cm. The maximum density remained at an almost constant depth (40–50 cm at 2 m from the trunk and 30–40 cm at 3m). The root density measured between 0 and 20 cm deep increased with the distance from the trunk.

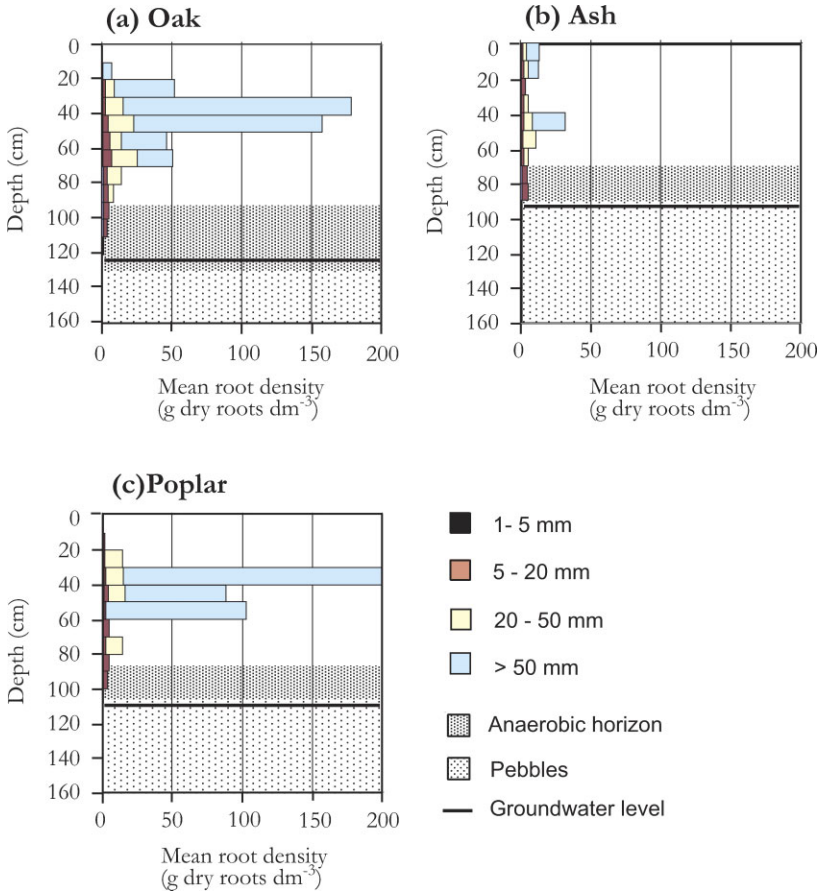

Figure 2. Rooting profile of oaks (a), ashes (b) and poplar (c) at 1 m from the trunk in grams of root per dm^3 of soil

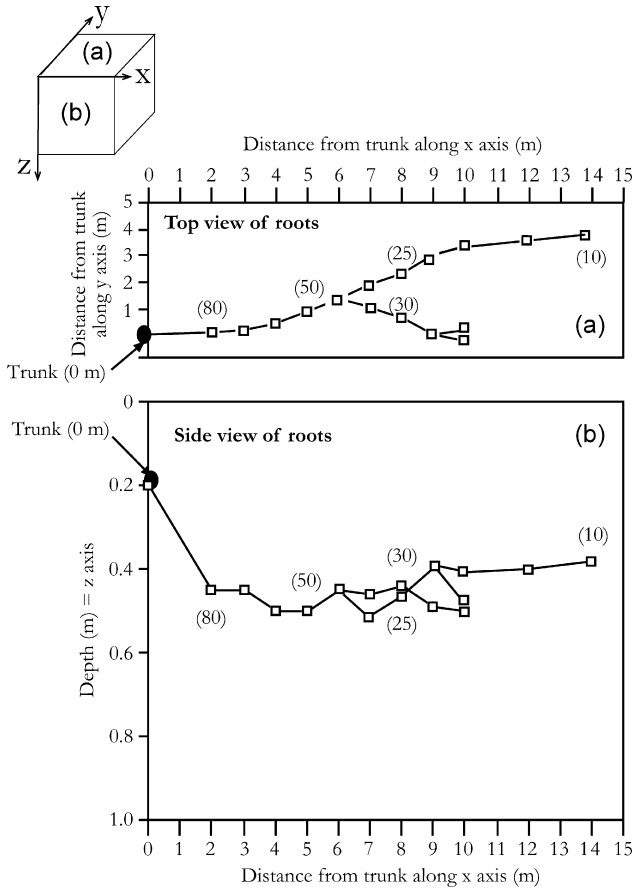

Figure 3. Top (a) and side view (b) of an oak root (on tree Q90) and main ramifications from the trunk to a distance of 15 m. Root diameter, in parentheses, is given in millimetres

Stable isotope measurements

The isotopic content of sap remained constant over the whole 24-h cycle: δ^{18}O-mean value (Q26): $-9{\cdot}8 \pm 0{\cdot}3$‰, δ^{18}O-mean value (Q90): $-9{\cdot}0 \pm 0{\cdot}3$‰, δ^{18}O-mean value (P77): $-8{\cdot}8 \pm 0{\cdot}3$‰. The low variations around the mean suggested that water uptake by the trees occurred at a relatively constant depth, because there was a steep and parallel decrease in ^{18}O in the roots and soil water down to 40 cm deep. Below this depth and down to the groundwater level, the isotopic composition of the root water did not vary significantly.

The isotopic composition of the water in a lateral oak root was constant over a distance of 3 m from the trunk at the same depth (Figure 4): the isotopic content of the soil water was horizontally homogeneous within the rooting area.

Sap fluxes

Mean xylem sap fluxes measured during the 2 days of root structure measurements (26–27 July 1996) per tree were 385 ± 41 l day^{-1} for oak, 472 ± 14 l day^{-1} for poplar and 221 ± 44 l day^{-1} for ash. The hourly maximum fluxes were 30, 27 and 13 l h^{-1}, respectively. In the roots the mean sap fluxes were 79 ± 27 l day^{-1} for oak and 67 ± 16 l day^{-1} for poplar. The total fluxes measured in the lateral roots represented 90% of the sap fluxes measured in the trunk of the two species, oak and poplar (Figure 5).

Leaf and soil water potential and soil moisture

The leaf water potential of oak and ash was $-0{\cdot}12$ and $-0{\cdot}31$ MPa, respectively, during the night, and $-2{\cdot}1$ and $-1{\cdot}9$ MPa at midday. The soil water potential measured 1 m from the trunk showed a zone of low water potential (-40 to -30 kPa) from 20 to 60 cm deep especially during the growing period (Figure 6). From a depth of 80 cm the water potential decreased down to the saturated zone. The soil water content down the section varied from 0·40 to 0·50 cm^3 cm^{-3} in the proximity of the groundwater table down to 0·20 to 0·30 cm^3 cm^{-3} in the rooting zone. The first 20 cm of the soil contained 0·30 to 0·40 cm^3 cm^{-3} water during the study period. The topsoil water potential varied strongly with the rainfall.

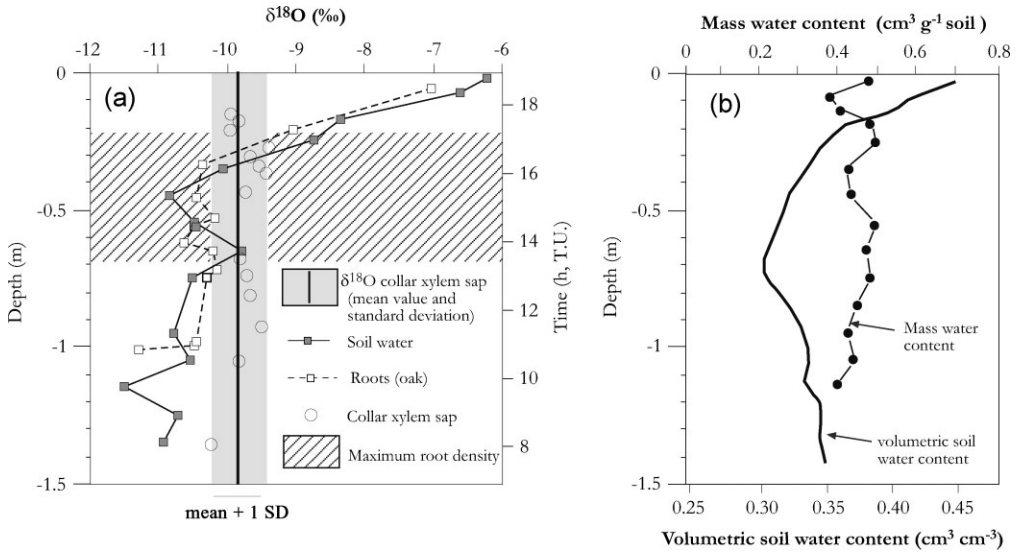

Figure 4. (a) ^{18}O content of oak root, trunk and soil water at different depths of the section. (b) Soil water content (per mass and per volume) versus depth

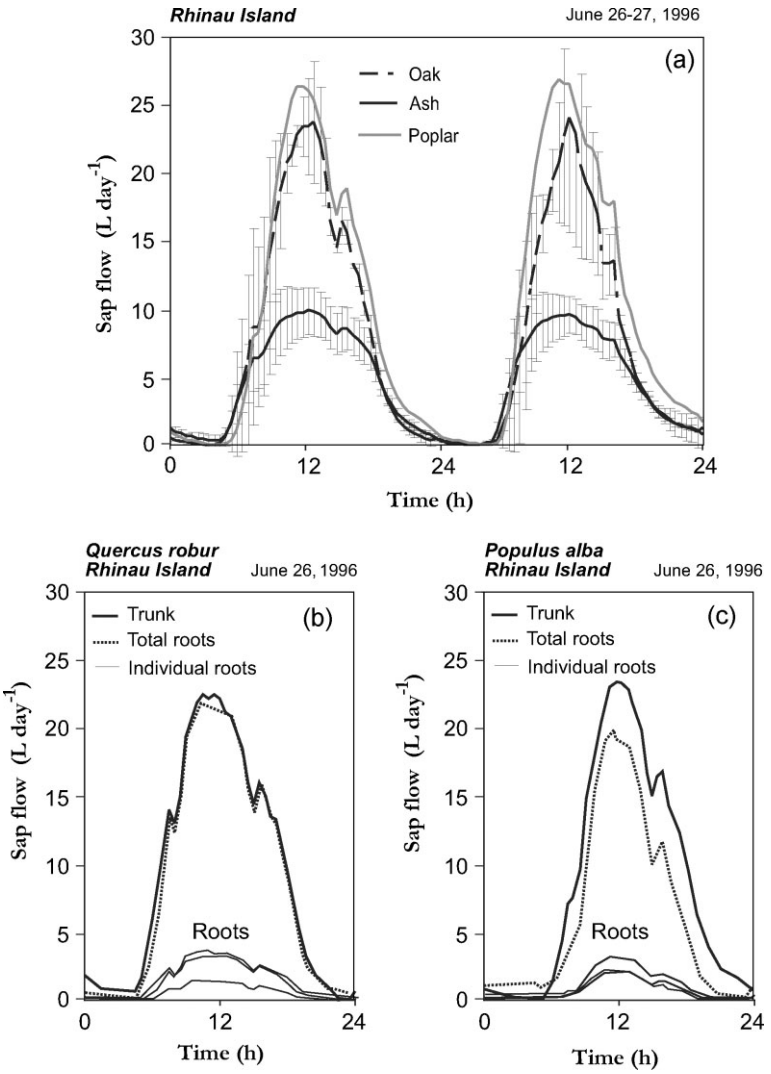

Figure 5. (a) Xylem sap fluxes in the trunk of oak, ash and poplar during the 2 days of the July 1996 campaign. Bars indicate standard deviation. (b) Xylem sap fluxes in the trunk (solid line) and roots (dotted line) of an oak (Q 90). The total root flux was calculated on the basis of three measurements of individual roots (thin lines) and extrapolated to all roots of the tree. (c) Xylem sap fluxes in the trunk and roots of a poplar (P77). Legend as for (b)

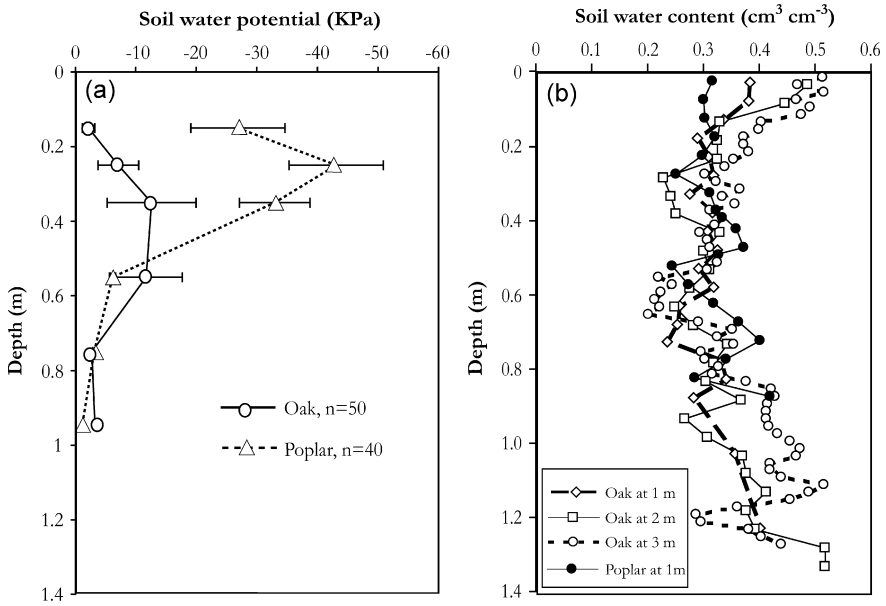

Figure 6. Vertical profiles of (a) soil water potential with standard error and (b) soil water content (measured on the day the trench was cut) at 1, 2 and 3 m from the trunk of an oak (Q90) and 1 m for a poplar (P77)

Water fluxes in soil varied from 1·5 cm day^{-1} during periods of rainfall to 0·3 cm day^{-1} during dry periods in summer (calculation from modelling of water flow in the unsaturated zone). The deeper soil layers (from 55 to 75 cm) were less influenced by the rainfall. During rainy periods, the water potential in the soil reached values close to zero (Figure 7). From 18 October, after leaf fall, the water potential of the soil remained constant, around −2 to −5 kPa.

DISCUSSION

Root density

In a forested alluvial environment with a water table close to the soil surface, the water supply for trees is a priori guaranteed. But a high water table can also be a stress factor for plants especially concerning oxygen availability (Pezeshki, 1994), trees therefore have to develop an adaptative strategy such as an adequate rooting structure.

The organization of the oak root system is little disturbed by the properties of the soil (Lucot and Bruckert, 1992). The root structure was of the with sub-horizontal taproot type, which reached depths of 60–70 cm and extended over 15 m from the trunk. The water table constituted the main obstacle to rooting, the minimum rooting depth being 1·2 m. It was noticeable that there were almost no roots in the first 20 cm. At 3 m from the trunk, roots only occurred between 30 and 80 cm deep. Between 5 and 15 m from the trunk, the root system was restricted to the 30–60 cm horizon. The architecture of the poplar root system was not very dissimilar to that of the oaks. This was reported elsewhere by Kostler *et al*. (1968). The differences concerned the maximum depth of the large sub-horizontal roots, which did not exceed 60 cm at 1m and 40 cm at 3 m from the trunk, and a denser colonization in the first 20 cm. Ash trees possessed a root architecture very different from that of oak and poplar. Roots were present in the whole depth of soil 1 m from the trunk especially between 0 to 20 cm deep and between 40 and 60–70 cm deep. This organization results from the presence of horizontal, oblique and vertical roots. The root system of ash trees was characterized by a sparse lateral extension, except for large roots close to the soil surface.

Thus, a complementary distribution of tree roots appeared in the alluvial soil of the riparian forests. In fact the ash tree rooted at the surface whereas oak and poplar roots spread a little deeper. For the ash, the lowest horizon was reached by the oblique roots which were damaged in the proximity of the saturated zone.

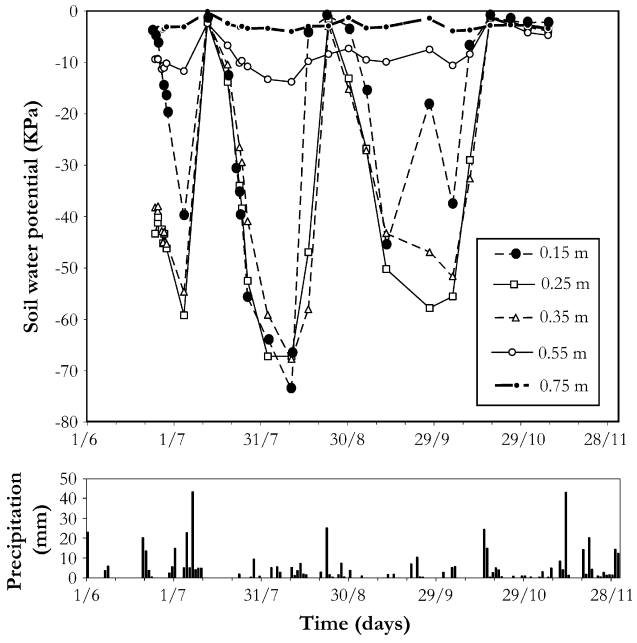

Figure 7. Soil water potential versus time at different depths in the soil 1 m from the trunk of Q90, in relation with precipitation, for the period 1 June to 28 November 1996

Root distribution and soil water profiles

In the alluvial environment, the hypothesis is that the water supply is derived from the groundwater (Busch *et al*., 1992) and that the root distribution is a priori a consequence of the distribution of water availability in the soil. However Plamboeck *et al*. (1999) found that water uptake by pines was more largely determined by the unsaturated hydraulic conductivity than by the root density.

The measurements of soil water potential profiles showed that the roots generated a zone of lower water potential at depths of between 20 and 60 cm. This is closely related to the water uptake by the trees. Moreover the water potential of the superficial layers was strongly controlled by rainfall events as also shown by Brodersen *et al*. (2000). During the episodes of rain or after leaf fall when transpiration is reduced, the water potential is close to zero in the topsoil whereas the water potential of the deeper layers close to the groundwater-table remains almost constant during all seasons. Water uptake by roots occurs in the unsaturated soil, in which there is the largest number of roots. The difference of the profiles of soil water potential (Figure 6) between oak and poplar are partly explained by the differences of root density. Between 10 and 30 cm, poplar roots are more numerous and the soil water potential lower, which was the result of the very active roots. Between 30 and 50 cm, the values of soil water potential were significantly different between these two species whereas root density was not. Note that on the whole profile very thin roots (<5 mm diameter) are more numerous for poplar than for the oak. At the lower levels, the tendency is inverted, oak roots being much more numerous and the soil water potential more negative than that measured at the same level for poplar. At depths below 70 cm, there was no link between the difference of root density and soil water potential. This can be explained by a reduced absorption and/or a fast supply of water to the root zone by capillarity.

Isotopic composition of soil and sap

The isotopic content of the tree sap reflects a mixture of groundwater and soil water taken up by the tree (White *et al.*, 1985). This mixing can occur as surface roots absorb soil water while deeper roots absorb groundwater. The relative amounts of soil water and groundwater taken up by a tree depend on the distribution of the roots in the soil and the availability of ground water to the roots. Thus, soil water would be expected to contribute significantly to the sap, even at wet sites where groundwater is easily accessible to the roots.

$$\delta^{18}O_{\text{sap water}} = \delta^{18}O_{\text{soil }1} D_{R1} + \delta^{18}O_{\text{soil }2} D_{R2} + \cdots + \delta^{18}O_{\text{soil}i} D_{Ri}$$

where $\delta^{18}O_{soil}$ is the isotopic composition of the soil water at different depths, D_R is the root density at different soil depths, $\delta^{18}O_{sap}$ is the calculated isotopic composition of sap: $\delta^{18}O_{sap}$ (Q26): $-10{\cdot}0‰$, $\delta^{18}O_{sap}$ (Q90): $-9{\cdot}1‰$, $\delta^{18}O_{sap}$ (P77): $-8{\cdot}8‰$.

With a high soil water content, the comparison between the measured (see $\delta^{18}O$-mean values in the Results section) and calculated values of the isotopic composition of sap therefore appear to be accurate. The isotopic ratios of trunk water were not the same as those of groundwater, but were closer to those of the more superficial soil layers. In these layers, the highest root density and high soil water content (around 50%) were found. However, the water available in the topsoil cannot be sufficient to explain sap flow without a continuous additional supply from the deeper layers. The water is provided by capillary action, favoured in alluvial contexts by the sandy-silt texture of the soil as confirmed by the low water potential of the soil.

CONCLUSION

By comparing the isotopic composition of water in the soil and the oak, it was concluded that the water was absorbed from between 40 and 60 cm deep, which is in good agreement with the distribution of the oak roots and the soil water potential. Thus, hardwood trees such as oak and ash take up water in the unsaturated zone, unlike softwoods (*Salix* and *Populus*; Busch *et al.*, 1992), which also used water from saturated zones. In this study the white poplar exhibited the same root extension as the oak. The root structure, and as a consequence the distribution of water uptake, could be an adaptative strategy of a riparian forest growing on more elevated stands than softwoods where the groundwater level is closer to the soil surface.

The analysis carried out following measurement of root structure, soil water, water potential, isotopic analysis and sap flux, allowed a scheme for the water movement in the alluvial forest ecosystem to be proposed (Figure 8): the root system works as a pump able to raise groundwater to the unsaturated zone by capillarity from the soil towards the superficial layers with a high root density.

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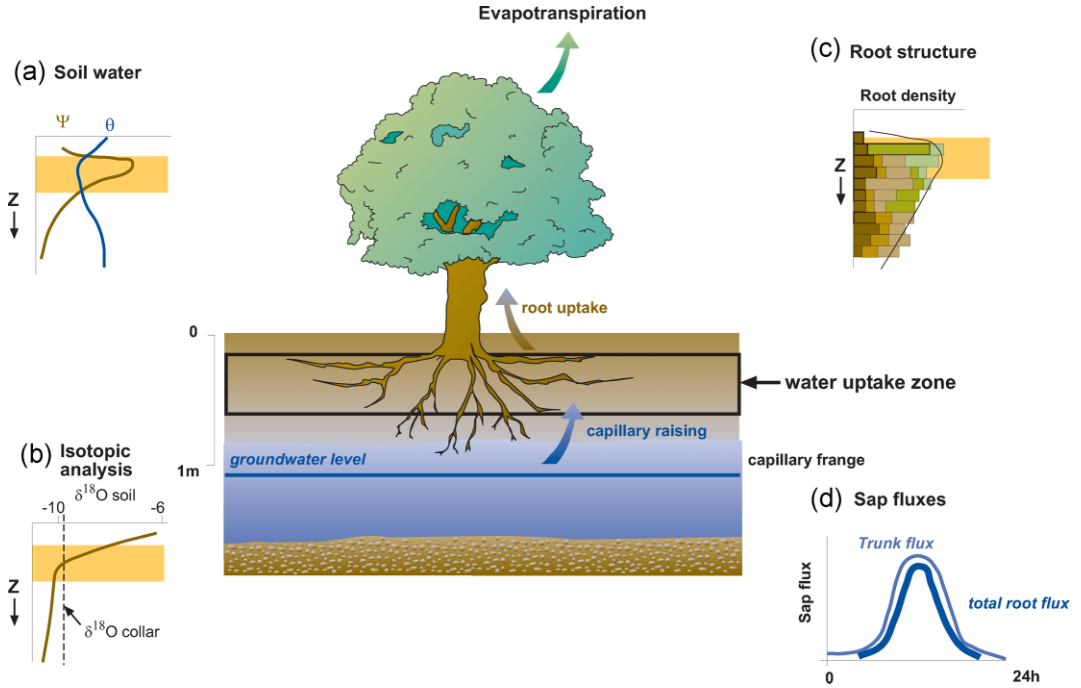

Figure 8. Scheme of water uptake by trees in the riparian forest. (a) Soil water content and water potential versus depth, (b) ^{18}O profile in the soil (dotted line shows $\delta^{18}O$ ‰ in the trunk), (c) density of roots versus soil depth and (d) sap fluxes in trunk and root over the 24-h cycle

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